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Title: Land sparing, land sharing and the fate of Africa's lions

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ACCEPTED VERSION PRIOR TO AMENDMENTS IN PROOF

Taxonomic bias in organismal research and conservation is well recognised, with focus disproportionately directed towards birds and mammals (1). Among mammals, carnivores often receive excessive attention and large carnivores are particularly well-studied (2). Papers reporting the population trends of a single species do not usually result in high profile publications, yet this issue of PNAS includes an analysis of population trends from across the global range of a large carnivore (3). To allay concerns that this is simply more evidence of taxonomic bias, some justification is required. Here, I argue that the work of Bauer et al. (3) goes far beyond documenting population trends in a single species – posing, instead, fundamental questions about how biodiversity should function and where it should occur in the landscapes of the future.

The once vast distribution of the lion (*Panthera leo*) (4) has contracted dramatically and, apart from an isolated population in India, the species is now restricted to sub-Saharan Africa. Within that range, habitat is highly fragmented and a previous, expert assessment identified 67 separate areas likely to contain resident lion populations (5). In their study, Bauer et al. (3) collated population estimates for 47 of these, representing all of the areas with repeated population estimates obtained by monitoring, and excluding only those for which estimates were based largely on extrapolation or expert opinion. Across these 47 areas, population estimates span an average of 13 years (range 4 to 47) with just over one estimate for every two years of monitoring. The data tell a bleak tale: lions in West and Central Africa, and those in East Africa are declining, and are projected to continue to do so by 50% or more over the next two decades. The majority of populations that have been stable or increasing are in fenced reserves found in just four countries in southern Africa.

For lion conservation, the implications of Bauer et al.'s study are sobering and should be influential. Importantly, they prompt the authors to call for the IUCN's red listing process to move towards regional assessments of endangerment, in line with the population divisions implied by recent phylogenetic studies (4). Nonetheless, this suggestion is most likely to interest those working on the conservation of large carnivores. So why does Bauer et al.'s study merit publication in PNAS, and what are the general lessons that it conveys? This question can be answered with regard to three topical issues in applied ecology and conservation.

First, a significant challenge in applied ecology is to ensure that biodiversity is monitored at scales relevant to the major processes that currently threaten

biodiversity and ecosystem function (6). In that context, Bauer et al.'s study stands out as a rare attempt to synthesise population trends from across the global range of a mammal, and for the rigorous approach employed to do so. In general, mammals are not as well monitored as some other taxa (such as birds (7, p8)). Much of what we know about mammalian population dynamics comes from intensive, long-term studies of specific populations. Such studies are profoundly insightful but, by their nature, shed relatively little light on spatially extensive processes like habitat loss and climate change. To tackle questions at such scales requires either standardised monitoring across large areas and time-frames, such as for many birds and butterflies in Europe (8, 9), or careful compilation of trends individually determined for different sites. Bauer et al. (3) exemplify the second approach: trend parameters have been determined from patchy and inconsistent monitoring data using a Bayesian hierarchical state-space model that allows for both process and observation error in the recorded abundances. With this approach, and by presenting the estimate of each population's trend as a probability distribution, Bauer et al. fully acknowledge the substantial uncertainty underlying data gathered from different parts of the lion's range.

Second, Bauer et al.'s study sheds light on the challenges facing species conservation more generally. The lion is iconic and, along with others of the "Big Five", emblematic of Africa's remaining megafauna. However, given the scale of the declines that Bauer et al. report, it is clear that neither its charisma nor its flagship status are sufficient to safeguard the lion from the threat of extirpation from across much of its current range. Highlighted threats include growing human populations in key lion areas, declining prey populations (which are tightly linked to predator abundance, especially for large carnivores (10)), and inadequate financial capacity to provide the required protection of lions, their habitat and their prey (3). These are salutary reminders that the processes of extinction seldom result from insufficient ecological understanding; rather, they are rooted in political instability, socio-economics, organised crime, and questionable political will to tackle the underlying causes of habitat loss and degradation (11–13). Bauer et al. point to the urgent need for increased funding to safeguard the lion. However, even intensive and financially demanding conservation programmes are struggling to arrest ongoing declines in other charismatic African megafauna (14). Additional finances might stem the rate of decline but, ultimately, political and economic solutions far beyond the scale of individual species are required.

Third, the findings of Bauer et al. (3) have a strong bearing on contemporary discussions about strategies for biodiversity conservation. Recent studies have assessed whether we should promote the existence of wildlife on land used for agricultural production ("land sharing"), or separate areas for human use from those for wildlife conservation ("land sparing"). These studies emphasise the efficiency of land use under the two models; in many cases, separating land uses is shown to be more efficient (15). However, studies of sharing and sparing have tended to focus on taxa that can fare well in relatively small tracts of spared land. By contrast, large carnivores and other large mammals need extensive areas to function properly. Sparing such extensive tracts is unlikely to be possible in many parts of the world, so we must usually choose between coexistence

(sharing lands with large mammals) and the confinement of species in areas too small for them to play a meaningful ecological role.

What is the evidence that coexistence with large carnivores is possible? Some regions are making progress (16) but coexistence is often uneasy and always under pressure. Even in those areas where carnivores are faring best, they are often limited by a deep-rooted human reluctance to share space with them. In the USA, wolves (*Canis lupus*) in the resurgent Rocky Mountain population are heavily culled outside protected areas, in spite of evidence that culling might actually increase their impacts on livestock (17). The wolf recovery in Scandinavia has been severely retarded by both legal and illegal killing (18, 19). In the United Kingdom, sharing pastoral lands even with badgers (*Meles meles*) is under threat; heavy culling of badgers is proposed, in spite of questions regarding its efficacy for limiting the incidence of livestock disease (20). These observations rob developed countries of the credibility to advise on coexistence. Bauer et al.'s finding that lions are declining in so many areas without intensive wildlife management also points towards an ongoing failure to achieve coexistence in Africa.

In the 1990s, Western & Wright (21) warned that, unless we could learn to share space with nature, we risked a future of nature "reduced and confined to hyper-managed ecological islands and megazoos". Causality is hard to identify but that lions are thriving in intensively managed and fenced reserves is a worrying indicator that Western & Wright's "megazoos" could dominate the lion's future in many countries. This is problematic, because the role of large carnivores in shaping the form and function of ecosystems is increasingly apparent (22). By restricting large carnivores to relatively small fenced areas, we leave nature outside shorn of a fundamental component of its natural state. At the same time, nature inside the fence is often dependent on culling, supplementation, and human-mediated genetic exchange. By these methods, we undermine the very notion of nature, and arguably fail in our mission to conserve.

The study by Bauer et al. (3) has important implications for the conservation of lions and of large carnivores more generally. In addition, however, it should cause a re-examination of what we believe to be nature and in what form we think nature should be conserved. If we are to avoid a heavy reliance on the confinement of unnatural nature, we must take inspiration from the smaller number of areas where Bauer et al. have shown that lions can thrive without fencing and intrusive management. Above all, we must consider whether we have the knowledge and the political will to conserve ecosystems with full trophic function and, if so, what currently limits progress towards that goal.

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Figure legend

Apart from a brief hiatus in the early 2000s, lion monitoring in Pilanesberg National Park, South Africa, has been conducted annually using rigorous and multiply-repeated aerial surveys. Since their reintroduction in the mid-1990s, lions have increased and now fluctuate in number between 40 and 60 animals (A). The Park is surrounded by fencing (B), which confers greater protection but, obviously, limits achievable population sizes. Burning (C) is conducted to stimulate new growth, increasing the carrying capacity of the area for lion prey. The thriving lion population (D) is a significant draw for tourists but, as with all fenced populations, requires active management of numbers. [Photo credits: (A,B) T.D.S. Docherty; (C) S.G. Willis; (D) P.A. Stephens]

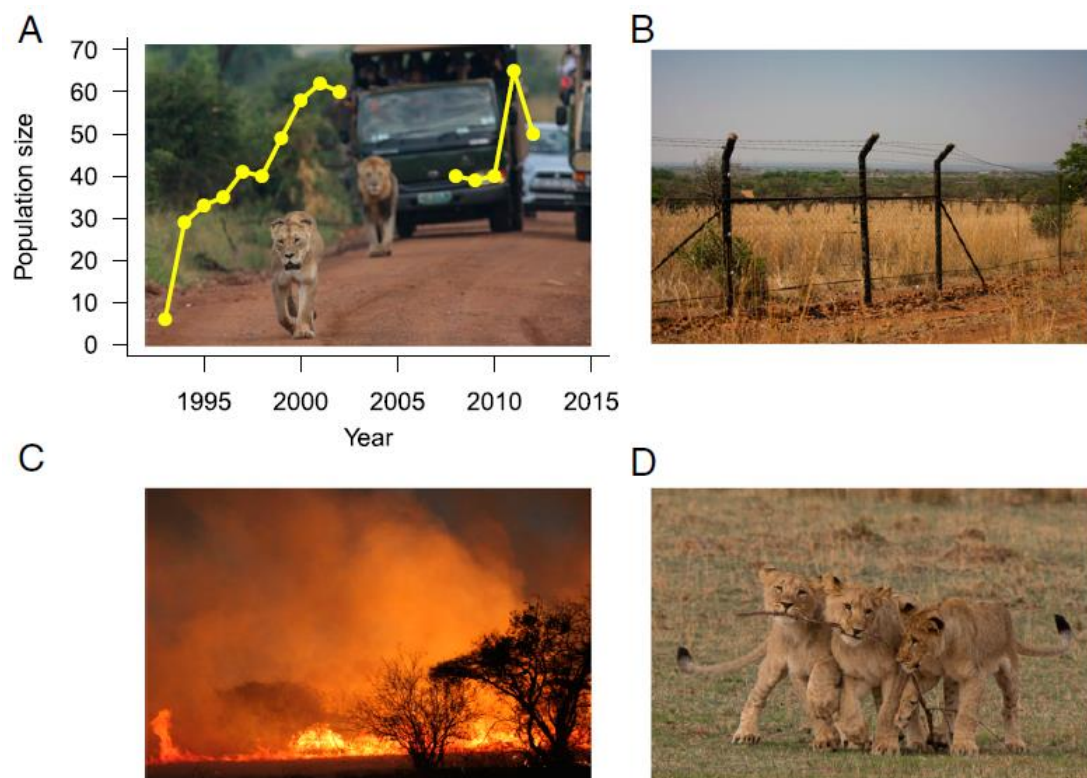


Fig. 1. Apart from a brief hiatus in the early 2000s, lion monitoring in Pilanesberg National Park, South Africa, has been conducted annually using rigorous and multiply repeated aerial surveys. Since their reintroduction in the mid-1990s, lions have increased and now fluctuate in number between 40 and 60 animals (A). The Park is surrounded by fencing (B), which confers greater protection but, obviously, limits achievable population sizes. (Photos courtesy of T. D. S. Docherty.) Burning (C) is conducted to stimulate new growth, increasing the carrying capacity of the area for lion prey. (Photo courtesy of S. Willis.) The thriving lion population (D) is a significant draw for tourists but, as with all fenced populations, requires active management of numbers. (Photo courtesy of P. A. Stephens.)